NUTRIENT CYCLING II : NUTRIENT DISTRIBUTION IN AMAZONIAN VEGETATION

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INTRODUCTION

The companion paper (Nutrient Cycling I. Nutrient Distribution in Some Amazonian Soils) describes the basis for this research and the type of study sites used for both the vegetation and soils studies. This work began during the 1967 expedition of the R/V Alpha Helix to the Amazon Basin. Observations of soils, roots, litter, and fungi resulted in the development of the "direct nutrient cycling hypothesis (Went and Stark 1968 a, b). This hypothesis states that on the poorest sandy soils in the Amazon, nutrients are transported from dead organic litter to living tree roots via mycorrhizal hyphae, thus bypassing the soluble and leachable phase in the soil.

Richards (1952), Sioli (1966), and others indicate that the Amazonian soils are highly leached and poor. This portion of the study was undertaken to determine how poor the vegetation was in ten biologically important elements relative to the soils from 12 study areas. If direct nutrient cycling does occur; it could be a response to exceedingly poor soils. If the litter is rich in biologically important elements and the soils are very poor, this would suggest the probable source of elemental uptake.

METHODS

Field Sampling Methods

Twenty individual litter fall plots one meter on a side were marked off with string following a random numbers system for the marked sections at Reserva Ducke and eight in the Rio Negro-Branco area. These were cleared of all organic matter to bare sand and the dry weight and elemental content (Cu, Fe, Mn, Zn, Na, K, Ca, Mg, N, P) of litter fall over 1,2,3,4,5,7,10 and 180 days were determined. The 1, 4, 5 and 7—day plots were sampled repeatedly.

A total of 20 random plots each 10 × 10 cm and adjacent to the litter fall plots were used for litter and soil samples for elemental analyses from four sites at Reserva Ducke. Five plots each were cut around a 10 × 10 cm template at Ducke A,

B and C, Borba, Rio Negro-Branco, second growth ("capoeira") at Rio Neg and two each at Aucayaco Lowland, Aucayaco Second Growth, Aucayaco *Lecyt* Copal Highland, LaMerced-San Ramon, and La Francia totaling 42 plots in The litter from each plot was severed at the plot boundary with a sharp knife a was oven-dried and stored for elemental analysis. The upper 4 cm with soil a roots were severed in the same manner as the litter. All roots between 0.05 a 1 mm in diameter were separated from the soil, washed, dried, weighed and sto for elemental analysis.

At the location of each plot, wood and bark samples (including cambi were taken from 2-3 m high on mature trees from 20 different living tree spec Bark samples were treated to remove epiphytes. These samples were dried were not homogenized for elemental analysis since the objective was to deter the natural range of variability of the elemental content of the rain forest soils.

At each plot, leaf samples from 20 different trees (in most cases leaf sam could be obtained only from near the ground) were collected between 10.00 12.00 and ovendried for elemental analysis.

Guha & Mitchell (1965) and Acquaye *et al.* (1964) noted differences in the mental content of different parts of leaves and different leaf positions on the t All Amazonian samples contained whole leaves (petiole and blade), and were sh and terminal in branch position. Leaves were separated into "young" (those r recently formed and turned green), and "old" (those with signs of age such as phytes, or those formed first). These samples were not homogenized in orde obtain a range of variability.

Notes were taken on the condition and types of plants, soils, and roots. S the objective was to study the over-all nutrient distribution in the compartm of the rain forest, collecting was not done by species but by compartments.

Elemental Analyses of Plants

All plant samples were dried at 65°C (±1°C) for 24 hours. Subsam were taken at random and these were homogenized by grinding in a mortar pestle. Because of the complexity of the native vegetation, and the proble obtaining identifications and shipping, material was not separated by species. data represent sample ranges of elements present in micrograms per gram of material for the compartments of the ecosystem.

All plant materials were predigested in duplicate with concentrated HN 180-200°C using 2 g samples in beakers. A tri-acid mixture of concentrat 10 parts HNO_3, 1 part H_2SO_4 and 4 parts $HClO_4$ completed the digestion. nearly dry digested material was taken up in triple distilled water to 50 ml vol

The total content of the elements Cu, Fe, Mn, Zn, Ca, and Mg was de ined using standard methods for a Perkin-Elmer atomic absorption spectrop meter (Willis 1963).

One percent lanthanum was used in samples and standards where Ca Mg were to be measured. The elements Na and K were measured fro tri-acid digestate using a Beckman flame photometer, and P was measured

rimetrically by the vanadomolybdophosphoric acid yellow color. Total nitrogen was determined by the Kjeldahl method (separate digestion).

RESULTS AND DISCUSSION

Litter Fall

Table 1 shows that an average of 5.7 g m^{-2} of litter falls to the forest floor in a day at Reserva Ducke in Brazil. Light litter fall here refers to leaves and small branches, but excludes tree trunks. Daily litter fall ranged from 4.6 to 6.3 g m^{-2}. Data covering one- to ten-day litter fall showed averages of 5.4 g m^{-2} day^{-1} of litter fall, but Table 1 shows that between 5 to 7 days, the weight of litter found on the

TABLE 1. *Grams of light litter fall (dry weight) per m^2 per day from Reserva Ducke and Rio Negro-Branco (65 samples)*

Time	Av.	Av.	Calculated g based on	
in Days	g $m^{-2}days^{-x}$	g $m^{-2}day^{-1}$	5.7$m^{-2}day^{-1}$	6g$m^{-2}day^{-1}$
1	5.7	5.7	5.7	6.0
2*	1.7	5.8	11.4	12.0
3*	14.3	4.6	17.1	18.0
4	25.2	6.3	22.8	24.0
5	30.7	6.1	28.5	30.0
7	34.8	4.9	39.9	42.0
10*	48.4	4.8	57.0	60.0

Av. 5.4 g/day for all days to 10
Av. 6.0 g/day for all days to 5

180 days (April-Sept.)	48.4g m^{-2} in 180 days or 0.26 g leaf fall m^{-2} day^{-1}. In 180 days 95.6% of the estimated leaf fall ($180 \times 5.7 = 1{,}026.0$ g m^{-2} $days^{-180}$) had decomposed leaving 4.4% behind. This was a loss of 0.55% per day over 180 days, or 5.4 g of litter was converted to mineral each day.

*Data limited to one or two measurements.

m^2 plots is significantly less than the calculated daily accumulation (5 to 7 $\times$ 5.7g). Data from 30 plots suggests that between 5 and 7 days, some decomposition of litter had begun, reducing the dry weight of litter. The average weight of litter fall for 1 to 5 days was 6 g m^{-2} day^{-1}(or 2,190 g m^{-2} $year^{-1}$, based on 44 plots) and probably represents the most accurate measure of litter fall. Table 1 shows that the first 5 days of measurements follow closely the calculated litter fall. More data should be collected, but these do give a good idea of what is occurring. The plot which lost 17% in calculated 7-day litter fall weight had a large number of soft fruits and flower parts (Table 1). These may have been decomposed by bacteria and

would be expected to lose weight rapidly. Since only a few fungal attachments were found on leaves left on the ground for 10 days during the dry season, it appears that the 5 to 7-day weight decrease may be partly the result of bacterial action, physical leaching and fungal action.

Litter fall by plots is extremely variable owing to differences in the canopy above. Plots located under palms or trees with broad leaves received a delayed leaf fall because of interception by the lower story. This explains the 4.6 g m^{-2} day^{-1} for the 3-day plots since these were located under palms. The calculated rate of leaf fall accumulation based on the averages for all time periods up to 10 days (5.4 g m^{-2} day^{-1}) falls consistently lower at most time intervals except for 3, 7, and 10 days suggesting that 5.4 g m^{-2} day^{-1} is too low a rate of accumulation because of oxidation and bacterial decay (Table 1). The 6.0 g m^{-2} day^{-1} (average of all data through 5 days) is a more accurate reflection of litter fall. From 2 to 5 days, the actual litter fall is slightly lower than or slightly higher than the N $\times$ 5.7g calculated level (N = number of days).

The rate of decay is calculated at 5.4g of the organic matter per m^2 converted to available mineral per day.

A daily loss of 5.4 g m^{-2} nearly equals the daily addition of 5.7 g m^{-2} day^{-1} litter fall in the tropics (Bray and Gorham 1964). By comparison the Amazon litter fall averaged 3,680 lb $acre^{-1}$ $year^{-1}$, while Cunningham (1963) estimated 8,000 lb $acre^{-1}$ $year^{-1}$ in Ghana, and 9,100 to 11,000 lb $acre^{-1}$ $year^{-1}$ were quoted by Laudelout & Meyer (1954) and others. The decomposition constant for the Amazon based on these data is 0.55%per day which is much lower than the 1.3%per day for Ghana (Nye 1961). Since the Amazon data represents only light litter fall during the dry part of the year, these data should be lower than the Ghana figures which cover annual branch and timber fall as well. The monthly Amazon litter fall data are considerably higher than the 21 g m^{-2} $month^{-1}$ reported by de la Cruz (1964) for Costa Rica.

The shallow depth of humus in the Amazon soils suggests that much organic matter is broken down and the by-products removed. If bacterial decay predominated with the aid of soil fauna, there would be an accumulation of humus to stain the surface sand. Such dark layers occurred only on very moist sites ("igapo"). Most sites had under 2 cm of humus.

Table 2 compares the amounts of various elements returned to the forest floor each day as litter fall based on 1- to 5-day figures. The ranges of elements vary considerably since some sites had mainly leaf and branch fall while others had high percentages of fruits or flower parts. The actual rate of litter fall for the 1-to 5-day period gives a more realistic picture of the elements returned from the canopy in litter than would the 1-day rate alone. In order to compare elements on a stoichometric basis, the data were converted to μe (microequivalents). The daily elemental return per m^2 for Cu was 0.9μe, for Fe 11.0μe, for Mn 2.4 μe, for Zn 2.6μe, for Na 278.6μe, for K 24.2μe, for Ca 660.0μe, for Mg 818.2μe, for N 25,344μe, and for P it was 35.8μe (Table 2). A total of 27,178 μe were returned to the soil surface daily in light litter fall.

Preliminary calculations showed that 0.86 μe Cu, 10.5 μe Fe, 2.3μe Mn,

TABLE 2. *Microequivalents and μg/g (dry litter) of elements returned in light litter fall each day, and calculated μe of elements per gram of dry matter released through decay per m² each day in the Amazonian rain forest, July-September*

Basis	Elements μg/g									
	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P
Average elements delivered in 1-5 days actual litter fall as av. $\mu g/g\ m^{-2}\ day^{-1}$	5.0	51.5	11.1	14.0	1,068	1,577	2,200	1,650	14,784	614
Above x 6.0 (av. grams of litter fall $m^{-2}\ day^{-1}$) expressed as total $\mu g/6g\ m^{-2}\ day^{-1}$	30.0	309.0	66.6	84.0	6,408	9,462	1,320	9,900	88,704	3,684
Above av. $\mu e\ m^{-1}\ day^{-1}$ elements added in litter fall	0.9	11.0	2.4	2.6	278.6	24.2	600.0	818.2	25,344	35.8
Calculated daily release of elements through decay of litter (95%) as $\mu e\ m^{-2}\ day^{-1}$	0.86	10.5	2.3	2.5	264.7	23.0	627.0	777.3	24,076	34.0

2.5 μe Zn, 264.7μe Na, 23.0μe K, 627.0μe Ca, 777.3μe Mg, 24,077 μe N, and 34.0 μe P were released from the organic matter of the forest floor on each m^2 per day and became available to the vegetation (Table 2). This is a far greater rate of release than could be expected of these soils with such low nutrient supplying power. These data are for April through September only. The actual daily rate may vary between the wet and dry seasons, and should differ for the various types of the Amazon.

Since the litter fall is regular, daily and sustained, it should provide the most dependable source of elements for rapidly growing vegetation. There is no way of knowing how much time is required for recharging the extractable levels of Na, K, Ca, and Mg on soil colloids or how much total soil mass represents the tree root zone.

Considering the moderately high levels of Na, K, Ca, and Mg which are released from the litter daily during the dry season, I would expect to find much higher levels of these cations in exchangeable form in the soil than actually occurred, unless direct nutrient cycling does predominate, or unless indirect nutrient cycling claims nutrients as soon as they are released. During the dry season, there was little leaching of elements in the soil because afternoon rains, when they occurred, were light (a trace to 1 cm). If the cations were released directly into the soil in soluble form, they should, in theory, accumulate near the surface. No such accumulations were found except in organic matter.

Elemental Analyses of Plants

Sixty pairs of subsamples from homogenized plant samples from different digestions were analyzed for the levels of Cu, Mn, Zn, Na, K, Ca, Mg, N, and P at separate times to determine the percentage of experimental error. Two elemental comparisons out of 60 differed by 4.7%, while all other comparisons differed by 0 to 3.8%. The average percent difference between duplicates was 0.95% on sixty samples.

The data were subjected to an analysis of variance, and results from paired comparisons were expressed as "x", significant at the 5% level, and "xx", significant at the 1% level. In view of the general problems of significance data and plant growth requirements; these statistics may not reflect whether certain levels of elements are significant to the growth or survival of the plants in different areas. Yet they are the only available data, and within the limitations of statistical analysis, they form a valid basis for conclusions, especially for the random plots at Ducke. Thus, the analysis of variance was applied as a general guide which indicates what differences of elemental concentrations are significant statistically. In Table 5, all comparisons which were significantly different at the 1% or 5% levels and those comparisons not discussed in the text were excluded because of the length of the tables. For example, most comparisons of Ducke A young leaves to Ducke B young leaves were excluded because fewer than three elements were significantly different. Significance tables for wood, bark, roots, litter, and litter fall are not included in this manuscript because of their length.

Comparison of Elements in Plant Parts

The analysis of variance compared leaves to wood to bark to roots and to litter for the level of significance of different elements and for individual sites. Since the data showing these comparisons are lengthy, a summary Table 3 is included to

TABLE 3. *Summary of results from analysis of variance and significance levels* (1% *and* 5%) *for elements in leaves, wood, bark, roots, and litter from the Amazon Basin (averages used in analysis were based on averages of* 20 *or more samples;* 0=*not significantly higher at either the* 5% *or* 1% *levels for any of the comparison*)

Location and Material	No. of times element was significantly higher of comparisons										Total No. Comparisons
	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P	
Peru											
Leaves				1		4	1	3	4	3	4
Wood					1	1					4
Bark					1	2	4		1		4
Roots		3		1	1		1				4
Litter		3	4				3	3	3	3	4
Brazil											
Ducke A											
Old Leaves	5		6	2		5	2	1	6	6	6
Young Leaves	6			5		4	4	1	5	6	6
Wood											6
Bark	1				1	2	6		1	2	6
Roots	2	6	1	6				3	1	4	6
Litter	1	6			4		2		1	1	6
Litter Fall (5, 7 days)	2		5		11		6	1	2	2	12
Ducke B											
Old Leaves	2			3		4	1	3	3	4	4
Young Leaves	3			3		4		3	3	4	4
Wood											5
Bark	1				2		4		1		5
Roots	1	5	3	3	5		1	2	1	3	5
Litter	1	2	5	2	2		4	3	2	1	5
Ducke C											
Old Leaves	1		3		1	4	2	4	4	4	4
Young Leaves	2		1			4	2	4	4	4	4
Wood											5

(Continued on next page)

Location and Material	No. of times element was significantly higher of comparisons										Total No. Comparisons
	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P	
Bark	1		1	1	5	3	5	1	1		5
Roots	1	5	1	4	1			1	1	3	5
Litter	1	4	4				2	3	1		5
Borba											
Leaves						2	1	1	2	1	2
Roots		2		2		1				1	2
Litter			1				1				2
Rio Negro-Branco											
Leaves	1		3	3		4	3	4	4	4	4
Wood											4
Bark					2		4	3	1		4
Roots	4	4		3	2			1	3	3	4
Litter		2	2	2	2		2	2	2	2	4
Brazil											
"Capoeira"											
Leaves	2					2	2		3	3	4
Wood											4
Bark	1					3	3		1	2	4
Roots	2	3	4	4	4	1			1	2	4
Litter	2	3	2	1			2	1	1	1	4
Totals											
Old Leaves	8	0	9	5	1	13	5	8	13	14	14
Young Leaves	11	0	1	8	0	12	6	8	12	14	14
Leaves	3	0	3	4	0	10	6	7	11	10	12
All Leaves	22	0	10	17	1	37	18	24	38	37	42
Wood	0	0	0	0	1	1	0	0	0	0	28
Bark	4	0	1	1	11	10	25	4	6	4	28
Roots	10	28	9	23	13	2	2	7	7	16	30
Litter	5	20	18	5	8	0	16	12	10	8	28
Litter Fall	2	0	5	0	1	1	6	1	2	2	12

show by sites how many times in the total number of comparisons a particular element from a certain plant part was significantly higher than the level of that element for the other plant parts under comparison. If a total of 4 comparisons were made covering averages of 20 samples, for example, Ducke A leaves to wood, leaves to bark, leaves to roots, and leaves to litter, and the leaves were significantly higher (1% or 5% levels) in a certain element for 4 out of 4 possible comparisons (averages

of 20 out of 20 samples), then this element must occur in high concentrations consistently in these leaves. Table 3 shows where the greatest proportion of individual elements occurs in the organic phase of the ecosystem although these data are not related to the total masses of organic matter which are present in the various plant parts in the ecosystem.

These comparisons show that on a gram for gram basis, wood was never significantly higher to any other plant part in any element (except for Na and K from Peru wood, Table 3).

Young and old leaves from Ducke A, B, and C were consistently higher than other plant parts in Cu, K, N, and P (Table 3).

Old leaves were most often higher than other plant parts in K, N, and P (Table 3). Young leaves were most often higher relative to other plant parts in Cu, K, N, and P as would be expected. All leaves regardless of age, were higher than all other plant materials in K, Mg, N, and P. Bark was high in Ca. Peru bark was significantly higher in most elements and had large numbers of epiphytes while Brazil bark was low in most elements and had mainly those epiphytes which have large catcher organs for catching debris and nutrients delivered from the air by rain. Roots were usually higher than other organic matter in Fe and Zn. Litter was variable, but often high in Fe, Mn, and Ca. Litter fall (5-day, 7-day) was consistently higher in Na relative to other plant material.

The Peruvian plant material studied varied less in elemental content among its different parts (leaves, wood, bark, roots, and litter) than did the Brazilian plant material and showed less tendency to concentrate elements except in leaves and litter.

Leaves

If young and old leaves from Peru are compared collectively to the same from Brazil, Peru had significantly higher levels of all elements except Na (Tables 4, 5). The Peru data used here do not include the data from limestone sites which had exceptionally high levels of Ca. This relationship of high Cu (range 0.5-22.5 μg/g), Fe (37.5-250.0 μg/g), Mn (2.9-47.5μg/g), Zn (27.5-87.4μg/g), K (4,000-20,000 μg/g), Ca (6,000-21,500μg/g), Mg (1.950-6,300μg/g), N(22,904-33,911μg/g), and P (2,700-5,050μg/g) and low Na (50-275μg/g) from Peru held true for most leaves from individual sites in Brazil as well as the sum of Brazil locations compared to Peru locations (Tables 4, 5).

Ducke A old leaves were higher in Mn, Ca, Mg, and P than were Ducke B old leaves (Tables 4, 5). The differences in elemental content of old leaves from A and B were expected since twenty species were sampled and some old leaves had abundant epiphytes while others had none and the two areas had slightly different vegetation.

Ducke C old leaves were significantly higher than Ducke B old leaves in Mn, K, Ca, and Mg (Tables 4, 5). The C site was high in organic matter and supported a wet site vegetation (igapo) while the A and B sites were dry. In general, the magnitude of differences in old leaves was not great for comparable locations in the Ducke area.

TABLE 4. *Average and ranges of elements in μ g/g for young and old leaves from the Amazon (based on 5 to 10 samples each, R=range, Av= average)*

Location		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P	Approx. %Ash	No. Samples
YOUNG LEAVES													
Peru	R	0.5—22.5	37.5—250.0	2.9—47.5	27.5—87.4	50—275	4,000—20,000	6,000—21,500	1,950—6,300	22,904—33,911	2,700—5,050	9.9—13.4	6
	Av	**11.8**	**131.7**	**17.7**	**37.6**	**188**	**14,018**	**14,286**	**3,456**	**23,892**	**3,790**	**13.2**	
Brazil													
Ducke A	R	4.8—15.0	37.5—55.0	0.5—17.5	13.1—37.5	50—595	1,625—9,375	750—4,000	1,300—3,300	21,208—38,891	2,120—2,600	1.4—5.5	5
	Av	**10.0**	**47.5**	**6.2**	**20.2**	**240**	**6,500**	**2,500**	**2,210**	**28,277**	**2,500**	**3.5**	
Ducke B	R	6.3—9.0	35.0—67.5	1.3—7.8	15.6—18.0	80—310	5,375—6,000	1,000—2,250	1,450—2,850	18,139—23,673	1,500—1,870	2.9—4.1	5
	Av	**7.2**	**51.0**	**3.8**	**17.1**	**186**	**6,825**	**1,740**	**2,060**	**20,291**	**1,680**	**3.4**	
Ducke C	R	4.8—8.8	32.5—47.5	4.8—9.8	10.8—15.0	75—245	10,750—12,500	2,000—5,000	1,500—3,600	15,526—23,673	1,330—2,750	3.6—4.5	5
	Av	**7.1**	**42.0**	**6.5**	**13.0**	**182**	**11,800**	**3,600**	**2,530**	**20,660**	**1,990**	**3 8**	
Borba	R	6.0—6.3	200.0—397.5	5.5—6.3	9.0—11.5	200—245	5,000—6,000	4,750—5,000	2,000 —3,150	21,982—22,904	1,380—1,380	3.4—4.8	3
	Av	**6.1**	**275.8**	**5.9**	**10.6**	**226**	**5,500**	**4,910**	**2,517**	**22,289**	**1,380**	**4.1**	
Rio Negro-Branco	R	11.3—12.5	72.5—130.0	6.0—8.0	16.5—20.0	100—113	12,250—13,250	1,000—1,000	6,500—7,000	—29,514	1,500—1,630	—	2
	Av	**11.9**	**101.2**	**7.0**	**18.2**	**107**	**12,750**	**1,000**	**6,750**	**29,514**	**1,570**	—	

TABLE 4. Contd. from p. 186

Location		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P	Approx. %Ash	No. Samples
"Capoeira"	R	12.0—	72.5—	9.5—	16.5—	100—	5,000—	9,750—	1,650—	23,827—	2,100—	5.6—	3
		15.0	77.5	12.5	17.5	125	7,125	10,250	1,800	23,980	2,600	7.2	
	Av	**13.1**	**74.2**	**11.4**	**16.8**	**108**	**6,333**	**9,417**	**1,717**	**23,882**	**2,280**	—	
OLD LEAVES													
Ducke A	R	3.8—	52.5—	6.0—	14.0—	180—	1,875—	2,000—	1,850—	15,526—	1,000—	2.1—	5
		12.0	67.5	34.8	20.0	489	6,875	5,000	4,150	23,980	2,500	4.9	
	Av	**7.4**	**53.0**	**17.3**	**16.8**	**336**	**4,050**	**4,000**	**2,780**	**20,409**	**1,610**	**2.7**	
Ducke B	R	6.3—	52.5—	1.5—	12.5—	125—	4,000—	2,100—	1,850—	15,987—	1,150—	3.0—	5
		8.8	62.5	15.8	18.8	370	10,625	3,250	2,300	23,827	1,750	5.2	
	Av	**6.9**	**57.5**	**5.2**	**16.2**	**216**	**5,925**	**2,520**	**2,100**	**20,137**	**1,410**	**4.3**	
Ducke C	R	6.3—	40.0—	6.3—	8.8—	233—	8,250—	2,900—	1,650—	19,676—	1,500—	3.7—	5
		7.8	92.5	15.3	23.3	443	9,500	4,500	3,050	21,982	1,800	5.0	
	Av	**6.6**	**57.0**	**10.6**	**17.7**	**336**	**8,650**	**3,830**	**2,600**	**20,413**	**1,590**	**4.4**	
TOTAL													
Brazil	R	3.8—	32.5—	0.5—	8.8—	50—	1,625—	750—	1,300—	15,526—	1,000—	1.4—	38
		12.0	397.0	34.8	37.5	595	13,250	10,250	7,000	29,514	2,750	7.2	
	Av	**7.8**	**73.4**	**8.0**	**16.4**	**299**	**7,450**	**2,956**	**2,641**	**22,875**	**1,810**	**5.0**	

TABLE 5. *Significance levels from analysis of variance of levels of elements (total) from young and old leaves and litter fall from the Amazon (based on 5 to 10 samples each, x= significant at the 5% level, xx = significant at the 1% level for comparison between paired items in brackets)*

Leaves	Elements									
	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P
Peru } **Ducke** }	xx	x	xx	xx		xx	xx	xx	x	xx
Brazil *Old Leaves*										
Ducke A } Ducke B }			xx				xx	x		xx
Ducke B } Ducke C }			xx			xx	x	x		
Leaves- Young										
Duck B } Ducke C }			x			xx	xx	x		
Leaves- Young, Old										
Ducke A, old } Ducke A, young }	x		xx		xx	x			xx	xx
Ducke A, old } Ducke B, young }			xx		xx	xx	xx	x		
Ducke A, young } Ducke C, old }	xx				xx	x	x		xx	xx
Ducke B, old } Ducke C, young }					xx	xx		x		xx
Ducke A, young } Ducke B, old }	xx								xx	xx
Ducke A, old } Ducke C, young }					xx	xx				x
Ducke C, old } Ducke B, young }			x		xx	x	xx	x		
Ducke C, young } "Capoeira" }	xx					xx	xx			
"Capoeira" Rio Negro-Branco }						xx	xx	xx	xx	xx

Only Ducke C young leaves differed significantly from Ducke B young leaves in Mn, K, Ca, and Mg (the same pattern which occurred between Ducke C and B old leaves, Tables 4, 5).

The old Ducke leaves (A-C) were significantly higher in Na (180-489μg/g) and lower in N (15,526-23,990 μg/g) than were the young Ducke leaves. Originally, I wondered if old leaves withdrew certain nutrients before being shed as is known to occur in many deciduous trees and shrubs in temperate climates where K, P, and N are transferred to branches. The evidence here is not conclusive, but there is a slight indication that they do conserve nutrients in this manner. Comparison of young to old leaves from different Ducke sites (Tables 4, 5) showed a tendency for old leaves to be higher in Na, young leaves to be higher in K and N.

Acquaye *et al.* (1965) studying cocoa leaves found an increase in Ca and Mg with greater leaf age, but it was not indicated if these data were significant. Older leaves decreased slightly in K, N, and P with age. Torne and Joshi (1964) found higher Na in older leaves of *Jatropha*.

The "capoeira" leaves were sampled in the fourth year after abandonment. Twenty tree species could not be found in the second growth so that samples represented results from *Cecropia* sp., *Triplaris* sp., *Heliconia* sp., and Melastomaceae. The "capoeira" leaves had similar levels of Cu, Fe, Mn, Zn, and Na to the neighboring Rio Negro-Branco leaves, with the former nearly always lower in elemental content (Tables 4, 5). The "capoeira" leaves were significantly higher in Ca and P than were the Rio Negro-Branco leaves. The extended direct nutrient cycling hypothesis stated that the "capoeira" vegetation is capable of concentrating certain elements which are essential to growth and readily lost to leaching. Calcium and phosphorus are two elements which might be readily lost from burned and cut-over land. The "capoeira" leaves showed high levels of Ca and P reflecting the apparent ability of the root systems of these plants to concentrate these elements. Since sampling was in the fourth year after abandonment, some leaves already shed during these four years may have held even greater concentrations of Ca and P, and perhaps of other elements as well. The fact that the "capoeira" leaves from plants on extremely poor soils had nearly as much of the remaining elements as the Rio Negro-Branco leaves, and slightly more Cu and Mn, suggests that the "capoeira" plants can concentrate these elements from the poor, leached soils which were low in Cu and Mn. The Rio Negro-Branco soils were richer (not significant at the 1% level except for Mg and N) in total Cu, Fe, Zn, Na, Mg, and N and in "available" Na, K, and Mg than were the "capoeira" soils, while both were nearly equal in Mn.

Neither mineral soil registered measurable levels of total P, but the "capoeira" surface soils were significantly higher in Ca and "organic" P than were the Rio Negro-Branco soils. The cutting and burning appears to have released much Ca to the "capoeira" soils which had adequate cation exchange capacity to hold the Ca which was ultimately concentrated by the plants. A closer study of the monthly changes of elemental levels in the plants and soils after burning is needed to complete the story. The "capoeira" plants do appear to be able to concentrate Ca and P with the aid of diffuse root systems. They may be able to concentrate other cations earlier after the burn; cations which have been depleted in available form after four

years and no longer can appear in high concentrations in the leaves. The rapid growth rate of "capoeira" vegetation probably aids in fast root growth and exploiting the soil for available cations as well as providing sizeable leaf area for concentrating and storing cations. Results from Guatemala soils (Snedaker and Gamble 1969) show much higher levels (than for Brazil soils) of extractable Ca, Mg, Mn, Na, and K in soils supporting second growth forest. The leaves from Guatemala second growth on these soils were similar to those in the Brazilian "capoeira" in N, P, Ca, but lower in K, and higher in Mg.

The ranges of elements found in leaves of *Fagus sylvatica* L., and *Aesculus hippocastanum* L. (Guha and Mitchel 1965), both temperate non-coniferous species growing on moderately rich soils, can be used as a general comparison for leaf elemental content between temperate and Amazonian areas. The range of Fe in the two temperate trees was 40 to 600 ppm, while most of the Brazil leaf samples showed 32.5 to 397 μg/g), or a generally low content considering the high levels of total Fe in the soil (600-1,700 μg/g). The Amazonian leaf samples, including Peru, were generally low in Mn (range 0.5-47.5 μg/g) compared to 20 to 1,000 μg/g for the temperate trees. Nearly all Brazilian and Peruvian rain forest leaves fell within the range of 10-100 μg/g Zn found in temperate trees. The Amazonian leaves held from 50 to 595 μg/g for Na which is quite low compared to 200 to 3,000 μg/g for temperate trees. Only a few leaf samples from the Amazon were below 5,000 μg/g (range 1,625-13,250 μg/g) which is low for K in temperate leaves (average, temperate zone 5,000-50,000 μg/g). A number of locations from the Amazon had leaves with under 2,000 μg/g of Ca, and none approached the maximum of 35,000 μg/g of Ca in temperate leaves. Nearly all Amazonian leaf samples fell above 1,000 μg/g for Mg, and below 4,000 μg/g maximum Mg found in the temperate trees, but the Peru leaves studied ranged above 1,000 μg/g. All Amazonian leaf samples were medium in P (1,000 to 5,050 μg/g) compared to 500-7,000 μg/g for temperate leaves. Only the Peru leaves came close to the maximum P content with most of the Brazil leaves falling below 2,600 μg/g. These data suggest that leaves grown on plants in the poor soils in the Amazon tended to be slightly lower to equal in elemental content to leaves grown on plants from richer temperate soils.

Most elemental analyses of leaves from the tropics deal with deficiency symptoms of tropical crop plants. For example (Acquaye *et al* 1965) 5,000 μg/g for K constitutes a deficiency condition in cacao leaves. Many of the Amazonian leaf samples approached or exceeded this level of K suggesting that the sites could support cacao without added K fertilizer, and in fact, this plant is a native in those areas.

The ash content of leaves was highest in Peru (13.2%), and ranged from 3.4-7.4% in Brazil leaves, in agreement with the difference in available soil mineral content.

Litter Fall

"Litter fall" included such things as small branches, bits of bark, flower parts, fruit and leaves in all stages of decomposition. Many leaves were held up in the canopy, especially in palm forests, and partly decomposed and leached above

ground. Thus, litter fall as used here has recently dead leaves as well as old leaves, but only light wood. The predecomposition in the canopy undoubtedly accounted for high levels of heavy cations in the litter fall after only 7 days. Fruit and flower parts caused sporadic high measurements of some elements (N, 46,270 μg/g, not averaged).

In theory, old leaves should have nearly similar nutrient levels to litter fall from the same general area since the old leaves soon abscise and become leaf fall and litter. In reality, litter and its accumulated products on the ground differs significantly after 5 or 180 days from old leaves, especially in Na, N, and P (Tables 4, 5 & 6). This is because some elements are withdrawn from old leaves before shedding, some leaching of suspended litter occurs in the canopy, and some of the litter fall is wood.

This decomposition may not necessarily be brought about by mycorrhizal fungi alone (during the dry season) because few fungal attachments to leaves could be found after either 5 or 7 days, but some forces must be at work digesting the leaves which were caught in the crown before falling to the ground.

Wood

Wood samples from Ducke A, B, and C did not differ significantly in three or more elements from one another. Ducke A, B, and C wood was significantly higher in Na, Ca, and N than was wood from the Rio Negro-Branco area (Table 7). Rio Negro-Branco wood was significantly higher in Mg than was Ducke wood. This is not surprising since the Ducke soils showed less extractable Mg and more Ca than occurred in Rio Negro-Branco soils. Wood from Peru (exclusive of that from limestone soils) was significantly higher in Cu, Fe, Mn, Zn, K, Mg, and P than wood from Ducke A, B, and C sites. This is consistent with the richer Peru soils. The Ducke woods tended to be higher in Ca (Table 7) than the Peru wood, which is not in agreement with the leaves from Ducke and Peru (Tables 4 & 5). The same relationship occurred between the Peru wood and Rio Negro-Branco wood, except that the latter was not significantly higher in Zn, but was higher in Mg than was the Peru wood. Peru wood was significantly higher in all elements (except Ca and N, (av. Ca 50 μg/g to 882 μg/g, "capoeira," and av. N 3,935 to 4,458 μg/g for "capoeira") than was the "capoeira" wood of Brazil.

Almost no data are available from the tropics for comparison of elemental content of wood, bark, or roots. A few measurements were made in Ghana, but few analyses are known from South America. Levels of elements are normally low in woods, and the Amazon woods fell generally slightly below to within the ranges of elements expected in temperate woods.

The ash content averaged lower in wood than in leaves. Wood ranged in ash content from 0.9-5.0% (Peru), and 0.5-1.9% in Brazil wood.

Bark

Only Ducke B and C bark differed significantly in three or more elements (Zn, K, Ca, Mg, N, all higher in C, Table 8). Since the C site was a wet "igapo" type of forest, it appeared to accumulate certain cations and N in the thick organic layer.

TABLE 6. *Averages and ranges of elements in μg/g for litter fall from the Amazon (based on 7 to 20 samples each, R = range, Av = average)*

Location		Elements μg/g										Approx. % Ash	No. Samples
		Cu	Fé	Mn	Zn	Na	K	Ca	Mg	N	P		
Brazil-Ducke													
5 days	R	5.0—	40.0—	6.3—	11.0—	200—	650—	500—	1,300—	11,375	300—	2.3—	10
		5.0	75.0	22.3	19.8	2,050	2,800	3,500	1,900	17,740	1,100	4.2	
	Av	**5.0**	**49.6**	**11.6**	**14.1**	**883**	**1,792**	**2,000**	**1,650**	**14,969**	**880**	**3.3**	
7 days	R	5.0—	47.5—	5.0—	7.8—	900—	900—	500—	1,200—	12,900—	250—	1.6—	20
		10.0	525.0	15.3	14.5	2,950	5,100	6,000	3,100	46,270	1,650	5.1—	
	Av	**7.8**	**139.2**	**8.9**	**11.5**	**1,500**	**2,850**	**3,305**	**2,083**	**14,324**	**760**	**2.9**	
Negro-Branco													
3 days	R	5.0	135.0	3.1	7.0	2,150	2,100	7,500	2,900	10,760	400	5.4	1
	Av	**5.0**	**135.0**	**3.1**	**7.0**	**2,150**	**2,100**	**7,500**	**2,900**	**10,760**	**400**	**5.4**	
4 days	R	7.5—	37.5—	3.0—	7.8—	2,350—	1,600—	500—	3,300—	12,300—	550—	4.3—	2
		7.5	45.0	3.0	8.0	2,450	2,950	2,000	3,700	12,300	750	7.7	
	Av	**7.5**	**41.2**	**3.0**	**7.9**	**2,400**	**2,025**	**1,250**	**3,500**	**12,300**	**650**	**6.0**	
7 days	R	13.8	140.0	3.8	8.0	500	2,950	8,500	3,400	—	650	5.9	1
	Av	**13.8**	**140.0**	**3.8**	**8.0**	**500**	**2,950**	**8,500**	**3,400**	—	**650**	**5.9**	
10 days	R	7.5	82.5	6.3	10.0	1,850	1,750	500	3,000	12,600	850	5.9	1
	Av	**7.5**	**82.5**	**6.3**	**10.0**	**1,850**	**1,750**	**500**	**3,000**	**12,600**	**850**	**5.9**	
180 days	R	11.3—	400.0—	21.5—	12.8—	50—	1,300—	7,000—	1,000—	9,070—	1,000—	4.6—	
		15.0	650.0	24.0	24.0	50	5,000	9,750	1,450	12,600	2,500	11.6	
	Av	**13.3**	**528.8**	**23.0**	**19.1**	**50**	**2,638**	**8,063**	**1,238**	**10,630**	**1,430**	**8.1**	
All Sites	R	5.0—	40.0—	3.0—	7.0—	50—	650—	500—	1,000—	9,070—	250—	1.6—	39
		15.0	650.0	24.0	24.0	2,950	5,100	9,750	3,700	46,270	2,500	11.6	
	Av	**7.7**	**154.4**	**7.4**	**12.9**	**1052**	**2,275**	**3,607**	**2,018**	**13,457**	**800**	**4.6**	

TABLE 7. *Averages and ranges of elements in μg/g for wood from the Amazon (based on 5 to 10 samples each, R = range, Av = average)*

Location		Elements μg/g										Approx. % Ash	No. Samples
		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P		
Peru	R	0.3—	1.3—	0.3—	1.9—	250—	250—	50—	180—	2,613—	100—	0.9—	7
		30.0	177.5	27.5	17.3	450	10,625	50	700	4,612	3,350	5.0	
	Av	**9.9**	**56.7**	**8.7**	**11.0**	**310**	**5,850**	**50**	**366**	**3,935**	**1,420**	**3.1**	
Brazil													
Ducke A	R	2.5—	10.0—	0.6—	7.5—	63—	1,250—	800—	250—	2,459—	100—	..	5
		2.5	12.5	2.1	12.3	250	3,000	1,175	400	3,228	250	..	
	Av	**2.5**	**12.0**	**1.4**	**10.4**	**133**	**2,120**	**975**	**290**	**3,062**	**160**	..	
Ducke B	R	3.8—	7.5—	0.8—	4.5—	475—	550—	375—	133—	3,536—	150—	1.9—	5
		3.8	7.5	1.8	5.5	700	1,375	1,075	275	5,073	400	1.9	
	Av	**3.8**	**7.5**	**1.2**	**5.1**	**520**	**960**	**690**	**203**	**4,138**	**260**	**1.9**	
Ducke C	R	2.5—	10.0—	0.8—	3.0—	138—	1,500—	850—	150—	2,877—	100—	0.5—	5
		2.5	12.5	1.1	5.0	303	1,500	1,025	250	4,150	350	0.6	
	Av	**2.5**	**10.5**	**1.0**	**3.4**	**245**	**1,500**	**965**	**210**	**3,316**	**180**	**0.6**	
Rio Negro-Branco	R	3.8—	12.5—	1.8—	4.8—	75—	1,100—	175—	500—	1,769—	100—	4.2—	5
		3.8	17.5	3.5	7.5	100	1,500	225	500	2,952	200	4.3	
	Av	**3.8**	**15.2**	**2.5**	**6.5**	**85**	**1,290**	**220**	**500**	**2,426**	**150**	**4.3**	
"Capoeira"	R	2.5—	12.5—	1.9—	3.5—	55—	2,000—	770—	150—	3,074—	100—	0.9—	5
		2.5	25.0	3.7	21.3	153	3,000	1,050	250	4,304	350	1.5	
	Av	**2.5**	**17.5**	**3.2**	**9.9**	**88**	**2,583**	**882**	**200**	**4,458**	**250**	**1.2**	**5**
Total Brazil	Av	**3.0**	**12.3**	**1.9**	**7.1**	**214**	**1,673**	**746**	**281**	**3,405**	**200**	..	30

TABLE 8. *Averages and ranges of elements in μg/g for bark from the Amazon (based on 5 to 10 samples each, R=range, Av=average)*

Location		Elements μg/g										Approx. %Ash	No. Samples
		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P		
Peru	R	0.3—	1.8—	0.8—	11.0—	200—	1,250—	10,000—	1,150—	7,071—	750—	10.1—	6
		22.5	14.5	23.8	41.8	500	12,875	25,500	2,875	14,989	9,000	17.4	
	Av	**8.3**	**36.6**	**7.6**	**21.9**	**360**	**9,458**	**18,250**	**1,729**	**11,545**	**1,260**	—	
Brazil													
Ducke A	R	6.0—	10.0—	3.5—	9.8—	400—	2,950—	6,500—	850—	12,144—	400—	2.6—	5
		6.3	15.0	4.5	12.3	1,025	3,225	10,000	2,150	13,988	550	3.2	
	Av	**6.2**	**12.5**	**4.3**	**11.1**	735	**3,088**	**8,000**	**1,313**	**13,037**	490	**2.9**	
Ducke B	R	5.5—	12.5—	2.5—	5.3—	475—	1,375	3,000—	250—	8,916—	350—	1.6—	5
		6.3	15.0	2.8	5.5	825	1,625	4,500	600	14,911	450	2.8	
	Av	**5.8**	**13.0**	**2.6**	**5.4**	**595**	**1,500**	**3,900**	**430**	**11,744**	**410**	**2.2**	
Ducke C	R	3.7—	17.5—	4.1—	15.8—	600—	3,875—	6,500—	850—	12,980—	250—	2.8—	5
		6.3	30.0	7.0	24.5	850	4,625	10,500	1,400	18,446	350	2.8	
	Av	**4.9**	**21.5**	**5.3**	**18.1**	**747**	**4,225**	**8,900**	**1,180**	**14,832**	**300**	**2.8**	
Rio Negro-Branco	R	6.0—	12.5—	1.3—	5.3—	200—	800—	1,150—	3,050—	5,688—	150—	1.9—	5
		9.5	25.0	7.3	7.0	325	1,775	1,450	4,050	7,225	350	4.1	
	Av	**7.7**	**17.5**	**4.3**	**6.3**	**258**	**1,317**	**1,350**	**3,467**	**6,802**	**250**	**2.9**	
"Capoeira"	R	5.0—	17.5—	2.8—	3.0—	25—	5,050—	7,500—	1,000—	10,760—	1,100—	1.1—	5
		7.8	40.0	22.5	8.0	85	5,875	13,500	1,850	15,526	2,150	3.9	
	Av	**6.6**	**28.5**	**7.2**	**6.1**	49	**5,460**	**10,000**	**1,510**	**12,120**	**1,640**	**2.2**	
Total Brazil	Av	**6.2**	**18.6**	**4.7**	**9.4**	**477**	**3,118**	**6,430**	**1,580**	**11,653**	**620**	..	25

"Capoeira" bark was significantly higher in Fe, K, Ca, N, and P than was Rio Negro-Branco bark from plants grown on adjacent soil. This relationship persisted even though "capoeira" soils were lower in Fe, the same or lower in K, higher in Ca, and much lower in N. Higher levels (compared to Rio Negro-Branco and Ducke Bark) of Ca and P were found for leaves, wood, bark, and roots for the "capoeira" area.

Peru bark was significantly higher than Ducke A, B, and C bark in all elements except Na and N. The same was true for Rio Negro-Branco bark, except that the Peru bark was highest of the two in Ca and not significantly different in Mg (Table 8). Bark had a higher average percent ash than wood. Peru bark had a range of 10.1-17.4% ash, while Brazil bark had an average of 1.1-3.9% ash.

Peru bark had significantly more of all elements than the "capoeira" bark except for Ca, Mg, N, and P. Considering the small soil differences, the bark of "capoeira" plants must be able to accumulate these elements.

Roots

Roots were the least variable in elemental content from site to site (Table 9). All of the comparisons between Ducke A, B, and C roots and Borba and Rio Negro-Branco roots showed no significant differences for more than one element. There is no explanation for such uniformity in the elemental content of the roots when other plant parts vary from site to site. It is possible that mycorrhizal roots are not selective accumulator organs as other plant parts appear to be. Uniformity is more surprising when the difficulty of removing sand grains and bits of organic matter are considered.

Measurements revealed the consistently and significantly higher levels of Na in the roots from Ducke B soils which were nearly the lowest of all soils in Na. This suggests an ability of the roots to accumulate Na which is readily leachable in soils low in this element (Table 9). Rio Negro-Branco roots were consistently high in Cu over all other Brazil roots (Table 9).

Peru roots were significantly higher (1% level) than Brazil roots only in Cu (av. 23.5 μg/g Peru to 9.7 μg/g Brazil) and in Ca (12,633 μg/g Peru, to 1,004 μg/g Brazil, an element which Peru soils and other plant parts have in large amounts except for wood).

This pattern is not consistent with that found for leaves, wood, or bark. The root elemental content was most unusual since all other Peru plant parts studied showed higher concentrations of all but Na compared to similar plant parts in Brazil. There is no good explanation for the difference in root behaviour from that of other plant parts, unless the roots are somewhat passive physiologically and the fungi govern uptake. The roots of some second growth trees do appear to have mycorrhizae adapted to nutrient uptake from mainly the soil. Soils which are quite different chemically have plants with roots which have nearly the same levels of elements.

The "capoeira" roots were consistently higher than were Ducke A-C roots in Mn, P, and to some extent in Zn (Table 9).

The soils of Rio Negro-Branco did not have roots with unusual concentrations of any elements, while the "capoeira" roots on poor soils had five elements (Mn,

TABLE 9. *Averages and ranges of elements in μg/g for roots from Amazon plants (based on 5 to 10 samples each, R = range, Av = average)*

Location		Element μg/g										Approx. % Ash	No. Sample
		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P		
Peru	R	0.5—	193.0—	2.5—	35.0—	100—	250—	4,000—	50—	11,068—	1,050—	8.2—	5
		52.5	875.0	11.3	77.5	550	4,750	20,000	3,900	21,521	2,100	18.6	
	Av	**23.5**	**480.0**	**5.6**	**52.0**	**383**	**2,167**	**12,633**	**1,550**	**15,139**	**1,550**	**13.1**	
Brazil													
Ducke A	R	7.3—	293.0	4.5—	21.3—	200—	1,500—	500—	1,000—	13,681—	750—	4.4—	5
		17.5	600.0	11.8	37.5	800	3,125	1,750	8,000	16,909	1,130	27.5	
	Av	**9.9**	**461.6**	**7.6**	**27.7**	**372**	**2,185**	**1,050**	**2,570**	**15,604**	**870**	**9.9**	
Ducke B	R	3.3—	160.0—	3.3—	9.3—	300—	1,250—	500—	1,050—	10,299—	700—	4.0—	6
		7.3	580.0	16.3	25.0	1,475	2,500	3,750	1,450	16,448	850	12.6	
	Av	**4.9**	**320.1**	**6.9**	**17.2**	**1,125**	**1,725**	**1,850**	**1,200**	**14,065**	**790**	**7.9**	
Ducke C	R	5.3—	115.0—	2.8—	8.7—	125—	350—	205—	350—	10,453—	600—	4.9—	6
		7.3	392.5	17.8	55.0	600	4,000	500	1,500	15,070	1,130	18.9	
	Av	**5.9**	**242.3**	**6.8**	**26.1**	**308**	**1,771**	**308**	**892**	**12,407**	**840**	**11.6**	
Borba	R	6.3—	297.5—	2.5—	19.5—	113—	1,500—	250—	1,100—	15,065—	930—	3.7—	5
		8.0	700.0	8.5	75.0	875	3,150	2,000	2,000	18,754	1,080	13.1	
	Av	**7.3**	**478.1**	**6.5**	**34.0**	**442**	**2,380**	**900**	**1,440**	**16,814**	**980**	**8.0**	
Rio Negro-Branco	R	13.8—	383.0—	3.5—	15.8—	200—	500—	200—	1,050	13,220—	700—	2.7—	4
		33.0	500.0	4.3	27.8	475	2,650	250	1,300	22,751	800	9.0	
	Av	**19.8**	**425.3**	**4.0**	**21.8**	**350**	**1,619**	**225**	**1,163**	**16,295**	**740**	**6.8**	
"Capoeira"	R	8.5—	368.0—	3.5—	18.8—	125	1,975—	750—	750—	11,529—	1,700—	5.8—	4
		12.5	532.0	29.3	57.5	475	5,500	3,750	2,300	16,448	2,250	25.7	
	Av	**10.3**	**463.7**	**16.6**	**44.0**	**319**	**3,244**	**1,688**	**1,488**	**13,988**	**1,900**	**1.26**	
Brazil Total	R	3.3—	115.0	2.5—	8.7—	113—	350—	200—	350—	10,299	600	2.7—	30
		33.0	700.0	29.3	75.0	1,475	5,500	3,750	8,000	22,751	2,250	27.5	
	Av	**9.7**	**341.3**	**9.4**	**28.4**	**486**	**2,154**	**1,004**	**1,459**	**16,100**	**1,020**	**9.0**	

Zn, Ca, K, P) present in significantly higher levels than did the neighboring forest. The general uniformity of the elemental content of largely mycorrhizal roots from the climax forest and the consistently higher elemental content of roots from the "capoeira" suggest a basic difference in physiology. Perhaps the plants which grow in the "capoeira" are those which can concentrate by diffuse penetration of the soil mass elements such as Mn, Zn, and K which are scarce in the leached soils, as well as Ca and P which are not as scarce as in neighboring soils, but must be bonded to soil or organic colloids. The elements accumulated by "capoeira" roots may become useful gradually to the returning climax forest through the fungi of their mycorrhizal root systems. Certainly more research is needed on the function of "capoeira" vegetation in the total picture of tropical succession.

"Capoeira" roots were significantly higher in percent ash (av. 12.6%) than were other Brazil roots indicating their tendency to accumulate elements. There are no similar elemental analyses of roots from tropical rain forest for comparison with these data.

Litter

Litter was extremely variable in elemental composition with wide ranges of elements. This is because it was never possible in the sampling used here to obtain exactly the same litter composition. Each section of forest floor receives a variety of litter from different species and in different stages of decomposition. Also, the litter fall varies in composition from day to day. Litter had variable depth, but did not include the humus (small fragments of material largely not recognizable as leaves). The separation of litter from humus in itself was subject to some variability. Litter contained variable percentages of small stem wood, bark, leaves, fruits, dead insects, fungi, and flower parts which added variability.

"Capoeira" litter, although sparse, was significantly higher in the heavier, less mobile cations, Cu, and Zn, while Ducke A, B, and C litter was higher in Na (Table 10). This implies that some part of the second-growth vegetation does concentrate these cations, but the mobile Na cations appear to be readily leached from exposed litter.

Peru litter reflected its richer soils and was higher than Ducke A, B, and C litter in all but Na (exception Ducke C, Table 10).

Data from Ghana (Nye 1961) indicated equivalent levels of K, Ca, Mg, N, and P or "fresh" litter from Brazil. Litter on the forest floor in Ghana averaged 4,500 μg/g K, 19,800 μg/g Ca, 2,400 μg/g Mg, 15,400 μg/g N, and 570 μg/g P. This compares to the following ranges of elements in Brazil litter: K, 500-2,650 μg/g; Ca, 500-9,000 μg/g; Mg, 650-7,500 μg/g; N, 9,990-40,736 μg/g (av. 15,314) and P, 100-1,100 μg/g (Table 10). For grounded litter, Ghana was higher in K, Ca, Mg, N, and below to slightly lower in P. The Ghana litter data reflected a rich vegetation and richer soils than occurred in the Amazon. Annual leaf fall data for Ghana and elemental return to the forest floor was much higher for Ghana than for the Amazon. The same elemental comparisons made for Peru and Ghana litter revealed that Ghana was higher in K, about the same in Ca, Mg, and N, while Peru litter was richer in P (Table 10).

TABLE 10. *Averages and ranges of elements in μg/g for litter from the Amazon (based on 5 to 10 samples each, R = range, Av = average)*

Location		Element μg/g										Approx. % Ash	No. Samples
		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P		
Peru	R	11.3—	342.5	8.9—	30.0—	50—	2,000—	7,500—	1,250—	14,900—	1,580—	11.3—	7
		22.5	550.0	87.5	50.0	245	6,500	32,000	7,460	25,671	5,250	20.8	
	Av	**14.8**	**440.0**	**51.1**	**35.3**	**110**	**3,679**	**17,071**	**3,566**	**20,921**	**3,920**	**16.8**	
Brazil													
Ducke A	R	4.8—	72.0—	3.1—	7.0—	495—	500—	1,425—	1,600—	13,374	200—	2.3—	5
		6.3	625.0	13.3	17.5	1,250	1,850	3,000	1,900	14,765	400	7.5	
	Av	**5.2**	**222.0**	**7.4**	**13.0**	**817**	**1,120**	**2,150**	**1,730**	**14,038**	**320**	**4.6**	
Ducke B	R	6.0—	40.0—	8.0—	7.0—	350—	575—	2,000—	950—	11,068—	100—	1.9—	5
		6.5	327.5	27.3	15.8	800	2,123	5,500	2,400	29,615	800	3.2	
	Av	**6.3**	**120.0**	**14.3**	**11.5**	**560**	**1,065**	**4,100**	**1,670**	**17,544**	**420**	**2.4**	
Ducke C	R	4.8—	40—	6.0—	5.5—	100—	575—	2,000	1,550—	12,298—	330—	2.5—	5
		6.3	222.5	19.0	20.0	675	2,500	5,500	2,225	40,736	530	4.6	
	Av	**5.8**	**135.5**	**13.2**	**12.4**	**290**	**1,245**	**3,900**	**1,815**	**14,180**	**410**	**3.5**	
Borba	R	6.0—	50.0—	4.3—	8.3—	250—	675—	2,000—	1,500—	11,216—	280—	3.2—	5
		10.0	195.0	17.0	18.0	700	2,225	7,000	3,150	20,137	700	6.3	
	Av	**6.9**	**123.5**	**10.9**	**12.9**	**345**	**1,225**	**3,700**	**1,940**	**16,967**	**520**	**4.4**	
Rio Negro-Branco	R	6.5—	50.0—	2.5—	8.8—	100—	800—	500—	1,850—	9,990—	330—	5.8—	5
		12.5	567.5	10.8	17.5	450	2,650	3,000	2,950	19,370	800	12.5	
	Av	**10.2**	**232.5**	**5.9**	**11.7**	**265**	**1,465**	**1,100**	**2,460**	**13,528**	**480**	**7.1**	
"Capoeira"	R	5.8—	125.0—	9.3—	13.5—	50—	800—	4,000—	650—	10,914—	750—	2.6—	5
		15·0	750.0	32.5	47.5	100	2,225	9,000	7,500	21,370	1,100	7.4	
	Av	**10.3**	**360.0**	**17.6**	**21.7**	60	**1,435**	**5,400**	**2,370**	**15,600**	**870**	**4.9**	
Brazil Total	R	4.8—	40.0—	2.5—	5.5—	50—	500—	500—	650—	9,990—	100—	1.9—	30
		15.0	750.0	32.5	47.5	1,250	2,650	9,000	7,500	40,736	1,100	12.5	
	Av	**7.5**	**198.9**	**11.6**	**13.9**	**389**	**1,259**	**3,392**	**1,997**	**15,314**	**500**	**6.9**	

Peru litter had the highest average ash content (16.8%) while Brazil litter ranged from 1.9 to 12.5% (av. 6.9%). "Capoeira" litter was lower (av. 4.9%) than Rio Negro-Branco litter (av. 7.1.%).

SUMMARY AND CONCLUSIONS

Observations in the Amazonian climax rain forest revealed a concentration of feeder roots in the surface 10 cm of soil with abundant hyphal and rhizomorph tissue connecting dead litter to living roots. Sections of roots showed that the majority of the roots in the climax forest had endotrophic mycorrhiza while those in the adjacent second growth "capoeira" forest had fewer of this type of mycorrhiza. These and other observations led to the development of a hypothesis which also has some support from the literature.

The direct nutrient cycling hypothesis states that nutrients are obtained from dead organic litter on the forest floor by mycorrhizal fungi which pass nutrients to living tree roots and may take substances from the roots. In second growth forests, the plants have diffuse roots which tend to concentrate nutrients dispersed through burning.

To explore the nature of nutrient cycling and nutrient reserves in the Amazonian ecosystems, twelve sites from five main areas in Brazil and Peru were sampled for leaves, wood, bark, roots, litter and litter fall. These samples were analyzed for the elements Cu, Fe, Mn, Zn, Na, K, Ca, Mg, N, and P using atomic absorption spectrophotometry, flame photometry and other methods. Data were subjected to an analysis of variance with significance levels of 1% and 5%.

An average of 6.0 g m^{-2} day^{-1} of litter falls to the forest floor in the Amazon and decomposes at the rate of 0.55% per day (valid for a site near Moura, Brazil). Each day 5.4 g of litter per m^2 is converted to minerals usable by plants. This rate of release would produce rich soils with fairly high levels of extractable cations if the minerals were released directly into the soil. Calculations show that 25,819μe of elements are released on each meter square of the forest floor daily, much more than the soils could supply through weathering or exchange capacity. Between 5 and 7 days, litter on the forest floor appears to begin to decrease in weight. Results point to the litter as a possible direct supplier of nutrients to roots in poor soils. Rainfall and deep roots add some nutrients to the system.

Old leaves from Brazil were consistently higher in K, N, and P than were other plant parts, while young leaves were higher in Cu, K, N, and P. Leaves from all sites and of all ages were higher in Cu, K, Mg, N, and P than were other plant parts. All plant parts were higher in all elements than was wood except for Na and K in Peru. Bark from all sites was consistently high in Ca, while roots had high levels of Fe and Zn. Litter was high in Fe and Mn. Old leaves showed a tendency to reduce their content of N before they are shed. Young leaves were usually higher in K and N while old leaves were high in Na.

The second growth soils were little different in elemental content from the adjacent Rio Negro-Branco soils, but leaves of the former concentrated significantly higher levels of Ca, and P while wood accumulated Zn, K, Ca, N, and P, bark accu-

mulated high levels of Fe, K, Ca, N, and P, and roots accumulated Mn, Zn, K, Ca, and P. The vegetation of the "capoeira" or second growth appears to be able to concentrate dispersed elements through its diffuse root system after burning. Temperate vegetation grown on rich soils tends to have higher nutrient levels than the vegetation on the poor Brazil soils.

Litter fall is variable in elemental content because of the varying proportions of leaves, wood, bark, fruit, and flower parts which compose litter. The heavier elements such as Cu, Fe, Mn and Ca tend to accumulate in older litter. These elements are probably not used as rapidly by the organisms of decay as are C, N, P.

Bark from the wet site (Ducke C) accumulated Zn, K, Ca, Mg, and N to levels significantly higher than found in bark of the surrounding vegetation. The high contents of elements in Peru bark correlates with abundant epiphyte growth while Brazil bark was poor in elements and low in epiphytes.

Roots were less variable in elemental content than were plant parts both in Peru and Brazil. Only the second growth roots held significantly higher levels of elements than other roots. This suggests that the second growth roots differ physiologically from the predominantly mycorrhizal roots of the climax forest.

Second growth litter differed significantly from other Brazil litter and had high levels of the heavy cations, Cu, Fe, and Zn even though the soils were low in these elements.

Leaves had the highest content of total elements of all plant parts with roots, litter, litter fall, bark, and wood next in that order.

Since the levels of extractable cations in the soil are very low, the Amazonian mineral spodosols studied could support only very limited growth. Dead organic litter provides the most concentrated and likely source of elements for plant growth. Radiotracer studies are in progress to determine if direct nutrient cycling does occur in nature. A careful study of all of the influences of cutting and burning in the Amazonian rain forest is needed. The sands of the Amazon Basin do not appear to hold promise as areas rich for agricultural development.

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